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Turning Body and Self Inside Out: Visualized Heartbeats Alter Bodily Self-Consciousness and Tactile Perception

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Abstract
Prominent theories highlight the importance of bodily perception for self-consciousness, but it is currently not known whether bodily perception is based on interoceptive or exteroceptive signals or on integrated signals from these anatomically distinct systems. In the research reported here, we combined both types of signals by surreptitiously providing participants with visual exteroceptive information about their heartbeat: A real-time video image of a periodically illuminated silhouette outlined participants' (projected, "virtual") bodies and flashed in synchrony with their heartbeats. We investigated whether these "cardio-visual" signals could modulate bodily self-consciousness and tactile perception. We report two main findings. First, synchronous cardio-visual signals increased self-identification with and self-location toward the virtual body, and second, they altered the perception of tactile stimuli applied to participants' backs so that touch was mislocalized toward the virtual body. We argue that the integration of signals from the inside and the outside of the human body is a fundamental neurobiological process underlying self-consciousness.

Keywords
cognitive neuroscience, consciousness, human body, virtual reality, vision

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Neurological, neuroimaging, and psychological data have highlighted the importance of bodily perception for a neurobiological model of the self and subjectivity. Inspired by early research on the body schema (Head & Holmes, 1911; Schilder, 1935), clinical researchers have recently described alterations of the self in cases of disturbed multisensory integration (Blanke, Landis, Spinelli, & Seeck, 2004; Brugger, Regrad, & Landis, 1997; Heydrich & Blanke, 2013; Heydrich, Dieguez, Grunwald, Seeck, & Blanke, 2010; Vallar & Ronchi, 2009). These insights inspired the use of multisensory conflicts to systematically alter the perception of the body and self (Blakemore, Wolpert, & Frith, 1998; Botvinick & Cohen, 1998; Dieguez, Mercier, Newby, & Blanke, 2009; Fourneret & Jeannerod, 1998; Lenggenhager, Tadi, Metzinger, & Blanke, 2007).

Alterations of the bodily self using multisensory conflicts have mostly affected isolated body parts—fingers (Dieguez et al., 2009), hands (Botvinick & Cohen, 1998), arms (Fourneret & Jeannerod, 1998), and the face (Sforza, Bufalari, Haggard, & Aglioti, 2010)—but can also induce changes in the perception of the entire body (Ehrsson, 2007; Lenggenhager et al., 2007). In one illusion (Lenggenhager et al., 2007), participants viewed their own body from behind while their back was stroked. With synchronous stroking, participants self-identified with the "virtual" body and mislocalized their self toward where the virtual body was seen.

In these studies on the bodily self, researchers manipulated only exteroceptive sources of information about the body (i.e., vision and touch). However, evidence has been put forward that the brain's representations of internal bodily states (interoceptive processes; e.g., Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004) are equally or

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even more important for the self (Craig, 2002; Damasio, 2000). Although recent work with a patient with bilateral-insula and anterior-cingulate-cortex lesions has suggested that exteroceptive and interoceptive signals can be integrated (Khalsa, Rudrauf, Feinstein, & Tranel, 2009), until now, no one has investigated how these signals interact to jointly affect bodily self-consciousness. This is surprising, given what is known about the convergence of visceral and somatosensory signals in single neurons in the spinal cord, brain stem, and thalamus (Foreman, Blair, & Weber, 1984; Takahashi & Yokota, 1983) and clinical data from patients with coronary heart disease and referred heart pain (Ruch, 1965).

We therefore developed an experimental setup to investigate whether a conflict between an interoceptive signal (the heartbeat) and an exteroceptive (visual) signal would modulate bodily self-consciousness and whether this "cardio-visual" conflict would also alter exteroception (tactile perception), as measured using the cross-modal-congruency task (Spence, Pavani, & Driver, 2004). We presented cardio-visual illumination of the virtual body in which a flashing silhouette was either temporally synchronous or asynchronous with respect to the participant's heartbeat. We predicted that participants would feel greater self-identification with the virtual body, that participants would self-locate more toward the virtual body, and that tactile stimuli would be mislocalized toward the virtual body more in the synchronous condition than in the asynchronous condition.

Method

Participants

Seventeen healthy right-handed participants took part (9 women, 8 men; mean age = 26.7 years, *SD* = 5.6 years). All participants had normal or corrected-to-normal vision and had no history of neurological or psychiatric conditions. They gave written informed consent and were financially compensated in return for participating. The protocol was approved by the local ethics committee—La Commission d'éthique de la recherche Clinique de la Faculté de Biologie et de Médecine—at the University of Lausanne (Lausanne, Switzerland) and was performed in accordance with the ethical standards laid down in the Declaration of Helsinki.

Materials and procedure

Setup, electrocardiogram (ECG), and signal analysis. The present protocol was an adaptation of an experimental setup that was previously used (Aspell, Lenggenhager, & Blanke, 2009; Ehrsson, 2007; Lenggenhager et al., 2007). Participants stood with their backs facing a video camera placed 2 m behind them. The video, showing the participant's body (virtual body), was projected in the *body conditions* in real time onto a head-mounted display worn by the participants (see Fig. 1). In the *object conditions*, participants viewed a real-time video of a rectangular object with height and width dimensions similar to those of a human body (see Fig. S1A in the Supplemental Material available online).

While filming the video, we also recorded the participant's ECG. Raw data (ECG) were acquired with the BioSemi Active II system (BioSemi, Amsterdam, the Netherlands) at a sampling rate of 2048 Hz. In-house software was developed to detect, in real time, the peak of each R wave from the ECG data and to trigger an additional visual stimulus (a flashing outline surrounding the participant's virtual body) that flashed on and off synchronously or asynchronously with respect to the participant's heartbeat (for further details, see Section 1 of the Supplemental Material). Note that it was only the synchrony of the flashing outline that was manipulated across blocks; the participant's body (or object) was always displayed in real time—that is, synchronously. Participants were not informed about the synchrony manipulation, nor were they told that the visual flashing was related to their heartbeat; however, there was an item in an administered questionnaire ("It seemed as if the flashing semitransparent template was my heartbeat"; see the following section and Table 1 for details) that alluded to this relation. We did not measure heartbeat awareness or sensitivity because doing so may have drawn attention to the synchrony manipulation. There were four blocks corresponding to four conditions: (a) *body synchronous* (BS; body with flashing outline synchronous with the heartbeat), (b) *body asynchronous* (BAS; body with asynchronous flashing outline), (c) *object synchronous* (OS; object with synchronous flashing outline), and (d) *object asynchronous* (OAS; object with asynchronous flashing outline).

Self-identification and self-location. At the end of each block, we administered an 11-item questionnaire adapted from Lenggenhager et al. (2007; see Table 1). The items were randomly ordered, and responses were made using 7-point Likert scales from −3 (*complete disagreement*) to 3 (*complete agreement*).

At the end of each block (duration = approximately 6 min), we measured self-location as described in Lenggenhager et al. (2007). Participants were passively moved backward 1.5 m (the experimenter gently guided the participants—who had their eyes closed—while they took very small steps). They were then asked to return to their initial position (with eyes closed) with normal-sized steps. The distance between the original position and the position estimated by the participant (drift) was measured.

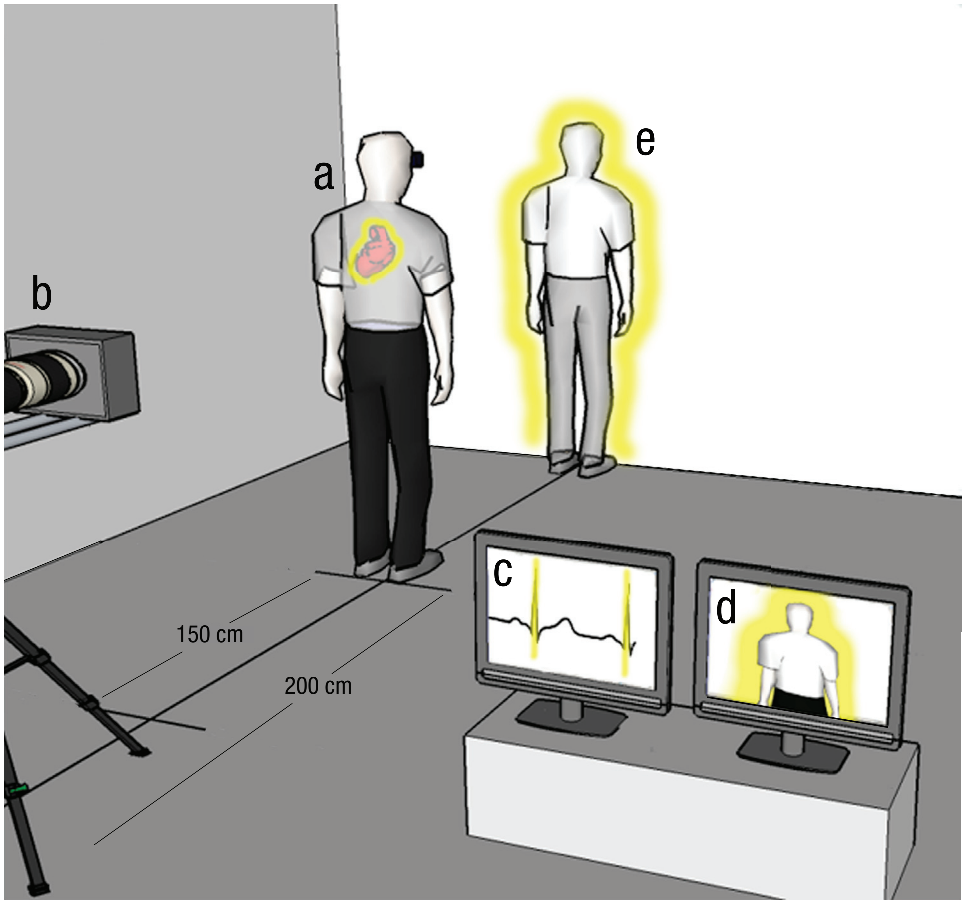

Fig. 1. Experimental setup for the body conditions. Participants (a) stood with their backs facing a video camera placed 200 cm behind them (b). The video showing the participant's body (his or her "virtual body") was projected in real time onto a head-mounted display. An electrocardiogram was recorded, and R peaks were detected in real time (c), triggering a flashing silhouette outlining the participant's virtual body (d). The display made it appear as though the virtual body was standing 200 cm in front of the participant (e). After each block, participants were passively displaced 150 cm backward to the camera and were instructed to walk back to the original position. See also Figure S1 and Movie S1 in the Supplemental Material.

Tactile perception: the cross-modal-congruency effect (CCE). To measure the effect of cardio-visual stimulation on tactile perception, we adapted our previous setup that allowed us to measure visuo-tactile CCEs (Aspell et al., 2009; for further details, see Section 1 of the Supplemental Material). In the cross-modal-congruency

Table 1. Questionnaire Items

1. It seemed as if I was feeling the vibration where I saw the virtual body/object.
2. It seemed as though I was in two places at the same time.
3. I felt as if the virtual body/object was my body.
4. It seemed as if the vibration I was feeling came from somewhere between my own body and the virtual body/object.
5. It felt as if my (real) body was drifting toward the front (toward the virtual body/object).
6. It appeared (visually) as if the virtual body/object was drifting backward (toward my body).
7. It seemed as if I might have more than one body.
8. It seemed as if the flashing semitransparent template was my heartbeat.
9. I felt as if my heart was in the virtual body/object.
10. It seemed as if I had two hearts.
11. It seemed as if I was feeling my heartbeat where I saw the semitransparent template flashing.

Note: Each of these items was placed in the following frame: "During the experiment, there were times when. . . ." Responses were made using 7-point Likert scales from −3 (*complete disagreement*) to 3 (*complete agreement*).

task, participants must make speeded judgments of the elevation of tactile stimuli while attempting to ignore visual distractors. The CCE can be used as an index of the perceived proximity of tactile and visual stimuli (Spence et al., 2004). The CCE was measured in both body and object conditions. Participants were instructed to keep their eyes open, fixate a location in the middle of their backs as viewed via the head-mounted display, and to wait for the first vibro-tactile and light-emitting-diode (LED) stimuli (presented 1 min after the start of the trial).

To measure the CCE, we used four light-vibration devices, each consisting of a small vibrating motor paired with a single bright LED. The two upper devices were positioned at the inner edges of the shoulder blades, and the two lower devices were positioned 9 cm below the upper devices. In the object conditions, the LEDs were taped onto the object at the same height from the ground and at the same relative distances as the vibrators on the participants' backs. Each trial consisted of a light (LED) flash followed by a vibro-tactile stimulus. The light-vibration devices from which the LED flashes and vibrations were emitted varied randomly and independently from trial to trial. Participants had to indicate, by pressing one of two buttons as fast as possible, whether they felt a vibration at the top or at the bottom of their backs (regardless of side) while trying to ignore the light flashes. There were four conditions (with 25 trials each), which differed in the relative locations of the target vibrator and the distractor LED: (a) same side, congruent elevation; (b) same side, incongruent elevation; (c) different side, congruent elevation; and (d) and different side, incongruent elevation. We analyzed reaction times (RTs) and accuracy in each condition.

Statistical analysis

To assess illusion strength, we first compared the subjective ratings for the illusion items (Items 1–3) with the ratings for the control items (Items 4–11) in the four experimental conditions using a two-tailed, three-way repeated measures analysis of variance (ANOVA) with body (body vs. object), synchrony (synchronous vs. asynchronous), and item type (illusion vs. control) as within-subject factors, following methods used in previous research (Morgan et al., 2011; Palluel, Aspell, Lavanchy, & Blanke, 2012; Slater, Perez-Marcos, Ehrsson, & Sanchez-Vives, 2008). To follow up on the ANOVA results, we carried out planned comparisons using paired *t* tests. On the basis of previous work (Botvinick & Cohen, 1998; Ionta et al., 2011; Lenggenhager et al., 2007), we postulated the a priori hypothesis of higher subjective ratings for the illusion items in the BS condition compared with the BAS condition and no such difference for the control items in the object conditions. We adjusted the significance level (alpha) used for multiple comparisons using the Bonferroni method ($p = .0125$).

In a second step, we focused on the differences among the ratings for the illusion items (in particular, Item 3: "I felt as if the virtual body/object was my body") by performing planned comparisons between the BS and BAS conditions, the OS and OAS conditions, the BS and OS conditions, and the BAS and OAS conditions using paired *t* tests. Again, we expected higher ratings in the BS condition compared with the BAS condition and generally higher ratings in the body conditions compared with the object conditions but no significant difference between the object conditions. Moreover, to check that the observed effects were not due to participants' awareness of the manipulation, we analyzed responses to Item 8 ("It seemed as if the flashing semitransparent template was my heartbeat") using the same contrasts. We adjusted the significance level using the Bonferroni method ($p = .003$).

We analyzed the drift (self-location) measures (calculated relative to the initial position = 0) using a repeated measures ANOVA with body (body vs. object) and synchrony (synchronous vs. asynchronous) entered as factors. We analyzed the RTs and the accuracy data of the cross-modal-congruency task using body (body vs. object), synchrony (synchronous vs. asynchronous), side (same side vs. different side), and congruency (congruent vs. incongruent) as factors. We here focus on the RTs rather than accuracy, given that RT data have been shown to be more sensitive for CCE analysis (Austen, Soto-Faraco, Enns, & Kingstone, 2004; Shore, Barnes, & Spence, 2006; Spence et al., 2004). Fisher's least-significant-difference test was used for post hoc testing, and the significance level used was $p = .05$. Three participants were excluded from CCE analysis (1 participant was excluded because of chance-level performance, and 2 participants were excluded because of technical problems). This resulted in a total sample of 14 participants for the CCE analysis. Trials with incorrect responses and trials on which participants failed to respond within 1,500 ms were discarded from RT analysis (Aspell et al., 2009; Spence et al., 2004). We also determined heart-rate variability from the ECG data by calculating the standard deviation of the average R–R intervals for each condition (Cowan, 1995) using repeated measures ANOVAs with body (body vs. object) and synchrony (synchronous vs. asynchronous) as the factors.

Results

Self-identification

The mean scores for Item 3 are shown in Figure 2a. We investigated the effects of seeing a body and synchronous cardio-visual stimulation on illusion strength

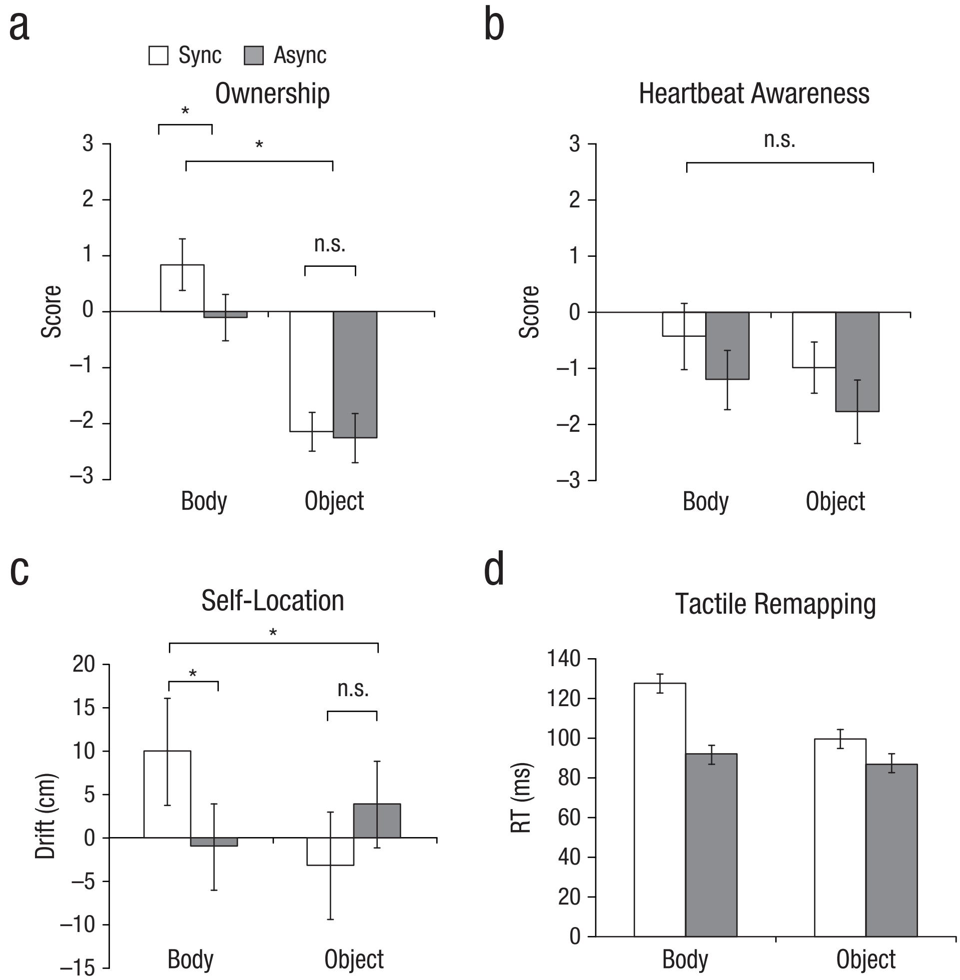

Fig. 2. Results. The graph in (a) shows mean scores for an item measuring self-identification (Item 3: "I felt as if the body/object was my body") as a function of condition. The graph in (b) shows mean scores for an item measuring subjective heartbeat awareness (Item 8: "It seemed as if the flashing semi-transparent template was my heartbeat") as a function of condition. The graph in (c) shows the average distance between the place where participants were originally standing and the place they moved to when asked to return there (drift, a measure of self-location), as a function of condition. Finally, the graph in (d) shows mean reaction times (RTs, a measure of the cross-modal congruency effect) as a function of condition. Error bars indicate standard errors of the mean. For a graph showing scores on all other questionnaire items, see Figure S3 in the Supplemental Material. Sync = synchronous condition; Async = asynchronous condition.

(average scores for Items 1–3) using a 2 × 2 × 2 repeated measures ANOVA. We found a significant main effect of body ($N = 17$), $F(1, 16) = 38.11$, $p < .001$, $\eta_p^2 = .704$; and item type ($N = 17$), $F(1, 16) = 13.14$, $p = .02$, $\eta_p^2 = .451$; as well as a Body × Item Type interaction ($N = 17$), $F(1, 16) = 20.1$, $p < .001$, $\eta_p^2 = .557$; and a Body × Synchrony × Item Type interaction ($N = 17$), $F(1, 16) = 4.36$, $p = .053$, $\eta_p^2 = .214$. Using planned comparisons, we showed with further analysis that the overall illusion was stronger in the BS condition than the BAS condition ($p = .01$, one-tailed). No significant differences between the average scores for the control items in the BS and BAS conditions or for any type of item in the object conditions were found (all *p*s > .08, one-tailed).

Subsequent analysis focusing on mean responses to Items 1 through 3 revealed that self-identification with the virtual body (Item 3; see Fig. 2a) was stronger in the BS condition ($M = 0.88$) than in the BAS condition ($M = -0.12$; $p = .002$, one-tailed) or in the OS condition ($M = -2.29$; $p < .001$, one-tailed), and stronger in the BAS condition than in the OAS condition ($M = -2.41$; $p < .001$, one-tailed). No significant difference was found between the OS and OAS conditions ($p = .33$, one-tailed). Analysis of scores for Item 8 revealed that participants were not aware of the experimental manipulation (mean ratings across all conditions were negative, and no significant difference was observed between the conditions; all ps > .07, one-tailed; see Fig. 2b).

Self-location

Cardio-visual signals also altered self-location (as shown in Fig. 2c): It was modulated by cardio-visual synchrony but only in the body conditions. Statistical analysis revealed no significant main effects of body ($N = 17$), $F(1, 16) = 1.10$, $p = .31$, $\eta_p^2 = .064$, or of synchrony ($N = 17$), $F(1, 16) = 0.38$, $p = .54$, $\eta_p^2 = .023$. However, statistical analysis did reveal a significant two-way interaction between body and synchrony ($N = 17$), $F(1, 16) = 8.93$, $p < .01$, $\eta_p^2 = .358$. This was caused by a significant difference between the BS condition ($M = 10.0$ cm; $SD = 24.6$ cm) and the BAS condition ($M = -1.0$ cm; $SD = 20.3$ cm; $p = .02$). Further analysis revealed that self-location differed from zero only in the BS condition ($p = .05$), not in the BAS condition ($p = .41$). In the object conditions, changes in self-location were smaller and did not differ from zero (all ps > .24); they also did not differ between the OS condition ($M = -3.2$ cm; $SD = 22.9$ cm) and the OAS condition ($M = 3.9$ cm; $SD = 22.4$ cm; $p = .11$).

Tactile perception

Figure 2d shows that CCEs were larger under conditions of cardio-visual synchrony. Statistical analysis revealed significant main effects of body ($N = 14$), $F(1, 13) = 8.73$, $p = .01$, $\eta_p^2 = .402$, and congruency, $F(1, 13) = 69.097$, $p < .001$, $\eta_p^2 = .842$, as well as a significant two-way Side × Congruency interaction, $F(1, 13) = 40.75$, $p < .001$, $\eta_p^2 = .758$, but no significant Body × Synchrony interaction, $F(1, 13) = 2.224$, $p = .16$. A significant three-way Synchrony × Congruency × Side interaction was also found, $F(1, 13) = 7.57$, $p = .02$, $\eta_p^2 = .368$ (see Fig. S2 in the Supplemental Material). No significant interactions were found among body, synchrony, and congruency, $F(1, 13) = 0.827$, $p = .38$, or among body, synchrony, and side, $F(1, 13) = 0.029$, $p = .87$. Furthermore, no significant four-way interactions among congruency, side, synchrony, and body were found, $F(1, 13) = 0.0302$, $p = .87$. For further discussion of CCE data, see Sections 2 and 3 of the Supplemental Material.

An ANOVA on the accuracy data revealed significant main effects of body, $F(1, 13) = 17.91$, $p < .01$; of side, $F(1, 13) = 16.52$, $p < .01$; and of congruency, $F(1, 13) = 21.5$, $p < .01$. There was also a significant Body × Congruency interaction, $F(1, 13) = 4.82$, $p = .04$, and a significant Side × Congruency interaction, $F(1, 13) = 6.55$, $p = .02$. No other main effects or interactions reached significance.

Further analysis revealed that these differences in tactile perception and bodily self-consciousness were not related to changes in heart physiology: An ANOVA comparing the heart-rate variability (standard deviation of the average R–R intervals) across conditions did not reveal any significant main effects or interactions among the BS (59 ms, $SD = 49$ ms), BAS (44 ms, $SD = 14$ ms), OS (59 ms, $SD = 58$ ms), and OAS (69 ± 85 ms) conditions (all ps > .33; see Fig. S2C in the Supplemental Material). Moreover, no significant main effects or interactions were found for the heart rate (R-peak-to-R-peak interval) among the BS (666 ms, $SD = 59$ ms), BAS (675 ms, $SD = 44$ ms), OS (684 ms, $SD = 59$ ms), or OAS (677 ms, $SD = 69$ ms) conditions (all ps > .4).

Discussion

The present study allows us to draw several conclusions. The data demonstrate that participants experienced stronger self-identification and a greater shift in self-location when an illuminating silhouette surrounding a video image of their body flashed on and off synchronously with their heartbeat. This is the first time that an extero-interoceptive conflict has been used to modulate bodily self-consciousness and tactile perception. In earlier studies, purely exteroceptive conflicts (Aspell et al., 2009; Lenggenhager et al., 2007; Zopf, Savage, & Williams, 2010) were used to manipulate bodily self-consciousness, whereas in a recent study, a type of extero-interoceptive conflict (attenuating tactile heartbeat sensations using a topical anesthetic) was used to enable investigation of the neural pathways mediating heartbeat awareness (Khalsa et al., 2009). Our findings are compatible with proposals that exteroceptive (Blanke et al., 2004; Blanke & Metzinger, 2009) and interoceptive signals (Craig, 2002; Damasio, 2000; Tsakiris, Jimenez, & Costantini, 2011) are important for the representation of self in the brain.

It has been proposed that the illusory feeling of ownership over rubber hands and virtual bodies (Botvinick & Cohen, 1998; Lenggenhager et al., 2007; Moseley, Gallace, & Spence, 2012) is at least partly explained by the fact that touch is inherently self-specifying sensory information (Bermudez, 1995) because tactile stimuli necessarily provide information about one's own body (whereas, e.g., visual signals do not). Interoceptive signals are also self-specifying sensory signals and, in addition, are *reafferent* signals, that is, afferent signals arising from the organism's own efferent processes—more specifically, arising from the organism's own visceral motor-control processes rather than from the external environment (Christoff, Cosmelli, Legrand, & Thompson, 2011). Given this, we argue that in conditions in which synchronous heartbeat-timing information is presented to the participant, albeit via an unusual route (vision), it increases self-identification with the virtual body relative to conditions in which the visual information is asynchronous.

We did not directly test interoceptive sensitivity (with a heartbeat-counting discrimination task), but we found no significant difference between ratings in the synchronous and asynchronous conditions for Item 8: "It seemed that the flashing semitransparent template was my heartbeat." Interoception can of course include cases of both conscious and nonconscious processing of heartbeat signals. Moreover, participants can sometimes perform above chance level on interoceptive "awareness" tasks, such as heartbeat-discrimination tasks (e.g., Critchley et al., 2004), even when they are not conscious of the heartbeat sensations (Ceunen, Van Diest, & Vlaeyen, 2013). Given the questionnaire data, it appears that in the present study, the nonconscious detection of heartbeat signals was driving the synchrony effects for most participants.

It is notable that these effects on bodily self-consciousness (self-identification and self-location) were observed only when the flashing outline appeared on a video image of the participant's body, not when it appeared on an object. The cardio-visual-synchrony effect is therefore not sufficient on its own to cause changes in bodily self-consciousness: The visual object must resemble a body. Similar findings have been reported by researchers using visuo-tactile stimulation of bodies (Lenggenhager et al., 2007) and hands (Haans, IJsselsteijn, & de Kort, 2008; Tsakiris, Carpenter, James, & Fotopoulou, 2010; Tsakiris & Haggard, 2005). Top-down mechanisms that refer to stored information about typical human body form are likely recruited for these illusions to occur: Multisensory congruence alone is not sufficient (Makin, Holmes, & Ehrsson, 2008; Tsakiris et al., 2010).

Our visuo-tactile CCE data extend our data on changes in bodily self-consciousness but also reveal different effects of cardio-visual synchrony on the CCE. By measuring the magnitude of the CCE (focusing on RT data) during cardio-visual stimulation, we directly tested whether cardio-visual signals would alter the perception of exteroceptive tactile cues applied to the body surface of participants during the illusion. On the basis of previous work showing that visuo-tactile stroking alters CCE magnitude (Aspell et al., 2009; Zopf et al., 2010) in conditions that induce changes in self-identification and self-location, we predicted that cardio-visual synchrony can induce similar changes.

Previous studies have shown that the CCE is sensitive to the perceived spatial proximity between the (tactile) targets and (visual) distractors by demonstrating that the CCE is larger—that is, visual interference in responses to tactile stimuli is greater—when the visual distractors and tactile targets are presented on the same side (closer to each other) than when they are presented on different sides. The condition with the greater perceived proximity between visual and tactile stimuli should show a bigger difference between same-side and different-side CCEs (Aspell et al., 2009; Pavani, Spence, & Driver, 2000; Spence et al., 2004). Our data revealed that the difference between the same-side and different-side CCEs was bigger and more significant in the synchronous condition than in the asynchronous condition and therefore show that the tactile stimuli were perceived as being closer in space to the visual distractors (seen on the virtual body or object in front of the participants) in the synchronous condition.

These CCE changes were of similar magnitude to those observed when the full-body illusion was induced using exteroceptive conflicts (Aspell et al., 2009); however, in contrast to the self-location and self-identification measures, the effect of cardio-visual synchrony on the CCE was present regardless of whether the participant's body or the object was viewed. On the basis of results from previous work in which visuo-tactile stimulation was used (Aspell et al., 2009), we predicted that CCE magnitude would have also been modulated by cardio-visual synchrony in a body-specific manner. In our previous CCE study, we found that CCE changes due to visuo-tactile stimulation were body specific; the lack of body specificity due to cardio-visual illumination in the present study was likely due to differences between the visuo-tactile and the cardio-visual conflict. Thus, during visuo-tactile synchronous stroking, stimuli that are felt on the participant's body are associated with what the participant sees on the virtual stimulus (body or object).

Synchronous visuo-tactile stimulation provides stimuli that are *temporally congruent* and *spatially incongruent* (because of the 2-m distance between the participant's body and where the filmed body is seen). In addition, the body conditions are *visually congruent* because the participant sees a body being touched (while the participant's body is touched). This is not the case in the object conditions: These are *visually incongruent* because the participant sees an object being touched while the participant's body is touched. During synchronous cardio-visual illumination, stimuli are also temporally congruent and spatially incongruent, as during visuo-tactile stimulation. Yet the stimuli are always visually incongruent—regardless of whether the body or the object is shown—because cardiac events are not perceived on the body as tactile cues are. Thus, in the case of cardio-visual illumination, body and object conditions are equivalent in the sense that both are visually incongruent. We argue that this accounts for the observed absence of the body-specific modulation of visuo-tactile CCEs in the present study.

The synchrony-dependent alteration in the spatial perception of tactile stimuli does, however, suggest that cardio-visual signals interfere with how tactile signals are integrated in the brain. The CCE data in the present study therefore also extend findings of cardio-tactile convergence in the spinal cord, brain stem, and thalamus and of the integration of cardiac signals with exteroceptive signals at higher, likely cortical levels of processing (Holzl, Moltner, & Neidig, 1998; Takahashi & Yokota, 1983). Viscero-somatic convergence has been observed in the spinal cord, the brain stem, and the thalamus, revealing single neurons with tactile receptive fields that also receive afferent cardiac input (Foreman et al., 1984; Takahashi & Yokota, 1983). Such convergence may account for the referred location of visceral sensations—for example, of heart pain—that are felt on the face (Ruch, 1965). Thus, afferent signals from the viscera converge with somatosensory afferents from specific body parts (Foreman et al., 1984; Holzl et al., 1998). Although we could not directly test this in the present study, we speculate that given the anatomy of the visceral and visual pathways, the present cardio-visual integration is supported by cortical (or thalamic) structures rather than subthalamic or spinal structures.

In conclusion, the present data on changes in self-identification and self-location suggest that mechanisms for detecting correlations between the timing of a flashing visual stimulus and the heartbeat are highly sensitive and are able to modify aspects of bodily self-consciousness. Our data show that internal and external states of the body are integrated and suggest that they converge within a common system representing the bodily self.

The brain's detection of correlations among multisensory signals is an important basis for distinguishing self from nonself (Botvinick & Cohen, 1998; Rochat & Striano, 2000; van den Bos & Jeannerod, 2002). In the present paradigm, we brought interoceptive cues to the "outside," which allowed us to induce a number of different fine-grained behavioral changes. Given that our data show that exteroceptive and interoceptive signals are combined and that they are potent modulators of bodily self-consciousness, we propose that signals from the inside and the outside of the human body form an integrated cortical system for bodily self-consciousness.

Author Contributions

J. E. Aspell, L. Heydrich, and O. Blanke designed the experiment. L. Heydrich, G. Marillier, T. Lavanchy, and B. Herbelin conducted the experiment. J. E. Aspell, L. Heydrich, and O. Blanke wrote the manuscript. J. E. Aspell and L. Heydrich contributed equally to the research reported here and should be considered as joint first authors. All authors approved the final version of the manuscript for submission.

Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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Supplemental Material

Additional supporting information may be found at http://pss.sagepub.com/content/by/supplemental-data

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